

Representation of Time by Neurons in the Posterior Parietal Cortex of the Macaque

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Summary

The neural basis of time perception is unknown. Here we show that neurons in the posterior parietal cortex (area LIP) represent elapsed time relative to a remembered duration. We trained rhesus monkeys to report whether the duration of a test light was longer or shorter than a remembered “standard” (316 or 800 ms) by making an eye movement to one of two choice targets. While timing the test light, the responses of LIP neurons signaled changes in the monkey’s perception of elapsed time. The variability of the neural responses explained the monkey’s uncertainty about its temporal judgments. Thus, in addition to their role in spatial processing and sensorimotor integration, posterior parietal neurons encode signals related to the perception of time.

Introduction

Many of the actions that we carry out on a daily basis are influenced by the ability to sense the passage of time. We must judge the duration of a signal light at a busy intersection, the time to strike a musical note, and the interval between our actions and their effects. Other animals besides humans also rely on a perception of time to coordinate their behavior (Gallistel, 2000). For example, the frequency that a foraging animal visits a potential food source depends on the amount of time between periods of food availability (Davison and McCarthy, 1988; Herrnstein, 1961). Thus, it has been argued that the computation of time represents an elementary aspect of cognition (Gallistel, 1990).

While experimental psychology has furnished many important insights about how animals encode temporal intervals, little is currently known about how the brain computes time or where in the brain time is represented (Buonomano and Karmarkar, 2002). Knowledge of temporal structure is likely to play a critical role in planning action, allocating attention, and forming decisions: when should a self-paced movement begin; when is sensory information relevant; by when should the evidence lead to a commitment to a particular behavior? These functions possess neural correlates in the sensorimotor association areas of the parietal and frontal lobes (Colby and Goldberg, 1999; Kim and Shadlen, 1999; Shadlen and Newsome, 2001; Tanji and Hoshi, 2001). Evidence from brain damaged patients and neuroimaging in normal subjects suggests that these struc-

tures may also play a role in time perception (Harrington et al., 1998; Onoe et al., 2001; Rao et al., 2001; Schubotz et al., 2000). As a first step toward elucidating the representation of time at the neuronal level, we recorded from cells in the lateral intraparietal area (LIP) of the rhesus monkey, a structure that is known to play a role in planning eye movements (Mazzoni et al., 1996; Platt and Glimcher, 1997; Snyder et al., 2000), directing spatial attention (Gottlieb et al., 1998), and forming decisions (Platt and Glimcher, 1999; Shadlen and Newsome, 1996, 2001). We designed a discrimination task that required the monkeys to plan eye movements based on their estimates of elapsed time.

Results

Time Discrimination by Monkeys

Two rhesus monkeys performed the time discrimination task shown in Figure 1A. The monkeys were required to determine whether a light (test cue) had been turned on for longer or shorter than a memorized standard duration. After a variable delay period, the monkeys indicated their answer by making an eye movement to one of two choice targets whose color indicated the designation “short” or “long.” The monkey’s performance is conveniently depicted by plotting the probability of a long report as a function of test cue duration (Figure 1B). The two psychometric functions shown in Figure 1B were obtained using standard cue durations of 316 and 800 ms. As these plots reveal, for the shortest and longest test cues, the monkeys performed the task nearly perfectly. However, for test cues near the standard durations, the monkeys’ performance was degraded.

The sigmoidal fits to these data (Figure 1B) furnished two parameters related to timing accuracy and sensitivity. The test cue duration at which short and long choices occur with equal frequency furnishes the monkey’s estimate of the standard duration, hence accuracy. We refer to this duration as the behavioral bisection point, τ_b . The test cue duration required to alter the monkey’s judgments from the bisection point to 75% long or short responses (i.e., 1/2 the interquartile range) provides an indication of the monkey’s sensitivity to the passage of time. We refer to this duration as the behavioral threshold, θ_b . In the experiment depicted in Figure 1B, the bisection points were 349 and 643 ms with the 316 and 800 ms standards, respectively. The corresponding thresholds were 93.3 and 110.8 ms. Values of τ_b and θ_b from 54 experiments are summarized in Table 1. Behavioral bisection points were near the two standard durations, and thresholds were greater (i.e., lower sensitivity) when the monkeys judged elapsed time against the longer standard.

It appears that the monkeys were less accurate when judging elapsed time against the longer standard. However, if behavioral thresholds are expressed as a fraction of the corresponding bisection points, the resultant average ratio (θ_b/τ_b) is similar for the two standard durations

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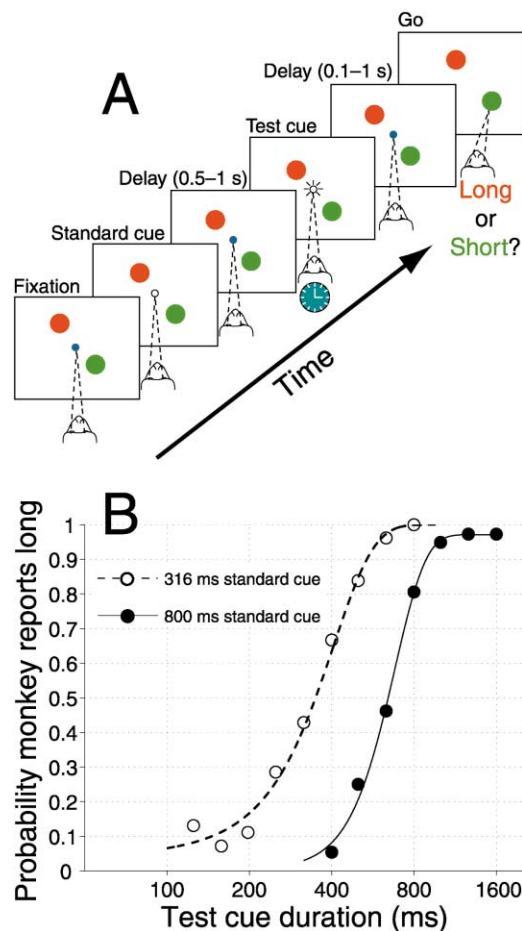


Figure 1. Time Discrimination Experiment

(A) Time-discrimination task. The monkey compared the duration of a test light (test cue) to a standard duration (316 or 800 ms). The test duration was selected randomly using intervals near the standard duration. After offset of the fixation point, the monkey indicated its judgment of the cue duration by making an eye movement to one of two colored choice targets. One of the targets was in the response field of the neuron. The monkey was rewarded for choosing the green target if the test cue was shorter than the standard, and for choosing the red target if the test cue was longer than the standard. Reward was administered randomly on trials in which the test cue equaled the standard.

(B) Behavioral results from one experimental session. Two standard durations were used in alternating blocks of trials, giving rise to the two psychometric functions. The probability that the monkey reported long increased with longer test cues. Sigmoid curves are best fitting cumulative normal distributions.

(see Table 1; $p = 0.11$, paired t test after log transform). This phenomenon, termed scalar timing or Weber's law for time, is well established in many species, including man (Gibbon, 1977; Rakitin et al., 1998). It indicates that uncertainty about time grows proportionally with the amount of time that has elapsed.

Time Discrimination by Neurons

We measured neural activity from area LIP of two monkeys while they performed the timing task. We screened neurons using a delayed eye movement task and selected for study those neurons with persistent activity before eye movements made to a region of space, termed the response field (RF) (Barash et al., 1991; Colby et al., 1996; Gnadt and Andersen, 1988; Platt and Glimcher, 1997, 1998). For example, the neuron in Figure 2B increased its response when the monkey was instructed to make an eye movement up and to the left of fixation but not down and to the right. The modulation of neural firing was evident within 100 ms of the appearance of the target and persisted until the eye movement. This pattern of activity was common for all of the neurons in our sample (Figure 2C), suggesting that these neurons represent the salience of a visual target that is the object of a future eye movement (Andersen, 1997; Colby and Goldberg, 1999). Our aim was to study these neurons during the time discrimination task, in which the passage of time would serve to instruct an eye movement toward one target versus another. By tying the salience of a target to the perception of elapsed time, we hoped to observe a neural representation of elapsed time in a structure devoted to sensorimotor integration.

Fifty-four neurons were tested on the time discrimination task. On half the trials, the short-choice target was positioned in the RF and the long-choice target was positioned in the opposite visual field. On the other half of trials, the target positions were reversed. The strategy allowed us to compare the neuron's response when the passage of time should decrease or increase the salience of the target in the neuron's RF.

The responses of many neurons appeared to correlate with the monkey's judgment of elapsed time. Results from a representative experiment are shown in Figure 3A. Early in the trial, the neuron responded more when the short-choice target was in its RF. The preference for the short-choice target was first apparent while the monkey viewed the standard cue and became more pronounced through the first delay period until the onset of the test cue. By the time the test cue first appeared, the response was 46.5 ± 2.3 spikes/s when the short-

Table 1. Behavioral and Neural Performance^a

	Bisection Point (ms) Mean (SE)			Threshold (ms) Mean (SE)			Ratio ^b Mean (CI)	
	τ_b	τ_n	$r_{b,n/TS}^c$	θ_b	θ_n	$r_{b,n/TS}$	θ_b/τ_b	θ_n/τ_n
316 ms standard	391 (9)	479 (26)	0.07	103 (5)	254 (35)	0.002	0.25 (0.22–0.28)	0.40 (0.30–0.53)
800 ms standard	728 (14)	775 (31)	0.15	165 (9)	419 (35)	0.11	0.22 (0.19–0.25)	0.47 (0.38–0.59)

^a $n = 42$ experiments in which bisection points were derived from the neural responses for both standard durations. Subscripts b and n refer to behaviorally and neurally derived values, respectively.

^b For the ratio of threshold to bisection point, we report geometric mean and 95% confidence interval (CI).

^c Correlation coefficients, $r_{b,n/TS}$, are for values obtained using the same standard duration. $p > 0.3$ for all correlations in table (Fisher z). Similar results were obtained when error trials were incorporated in the analysis.

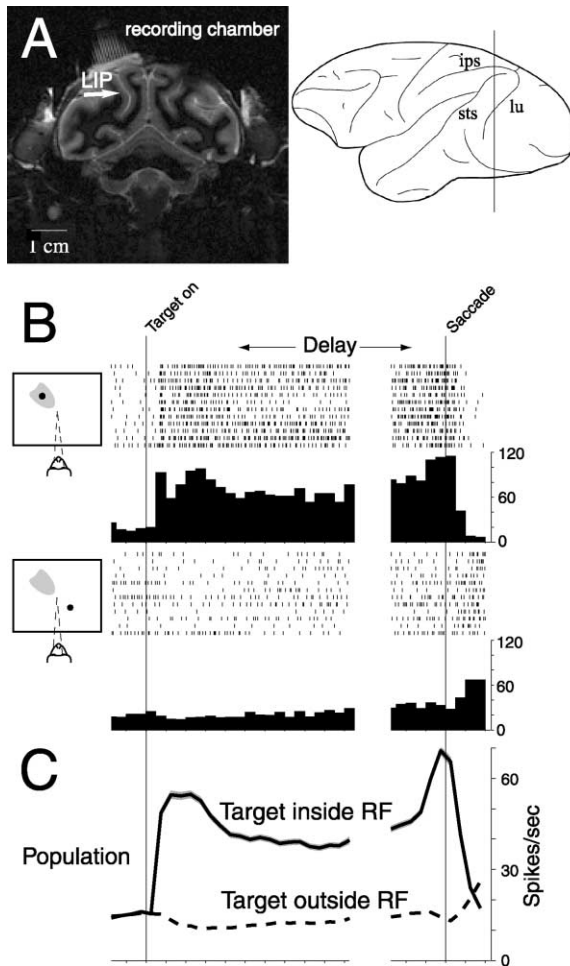


Figure 2. Location of Neurons and Screening Procedure

The data set consists of 54 neurons from the ventral portion of the lateral intraparietal area (LIPv). All neurons exhibited spatially selective persistent activity during an instructed-delay eye movement task.

(A) Magnetic resonance image. The recording cylinder is shown above the intraparietal sulcus (ips). Insert shows the coronal plane of the MRI containing most of the neurons described in this report. Most neurons were within ± 2 mm of the arrow, along the lateral bank of the ips.

(B) Responses from one neuron on the eye movement task used for screening. The neuron emitted a persistent train of action potentials when the target instructed an eye movement into the response field (gray in cartoon). Rasters and average response plots are aligned to two events in the trial. On the left, responses are aligned to the onset of the target that served as the instruction; on the right, responses are aligned to the onset of the monkey's eye movement. The target was visible for only 200 ms.

(C) Response averages for 46 neurons that were tested on the delayed saccade task. Tick marks on the time axis denote 100 ms increments. An additional eight neurons were screened informally.

choice target was in the RF, compared to 25.5 ± 1.7 spikes/s when the long-choice target was in the RF (spike rate \pm SEM, computed in 50 ms epochs). As the duration of the test cue neared the standard, the difference in activity diminished and eventually reversed to favor the long-choice target. By the end of the longest test cue, the average response was 57.4 ± 4.4 spikes/s when the long-choice target was in the RF, compared

to 44.7 ± 5.3 spikes/s when the short-choice target was in the RF. When the standard duration was reduced to 316 ms, we observed a similar pattern of activity from this neuron, albeit shifted to an earlier time (Figure 3B).

This crisscrossed pattern of neural activity was evident across the population. Figure 3C shows the time course of activity from all 54 neurons on correct choices using both standard durations. At the beginning of the test cue period, the activity favored the short-choice target. This is remarkable because, at this point in time, the likelihood that the monkey will experience a short or long duration cue is equal. This preference for the short-choice target gradually gave way to the opposite preference for the long-choice target if the test cue was sufficiently prolonged. This change in preference from the short- to the long-choice target occurred later in the blocks of trials in which the monkey compared elapsed time to the longer standard (solid curves).

The population response also exposes the gradual change in neural activity that accompanies the passage of time. This is best supported in the portion of the graph corresponding to the longer cue durations, when the test cue exceeded the standard duration. Although all of the trials comprising this portion of the curves culminated in a long choice, there was a gradual increase or decrease in the average spike rate which accompanied the passage of time ($p < 10^{-7}$ for all four cases; weighted least squares regression). The gradual changes in activity accompanying cue durations longer than the standard cannot be attributed to changes in the monkey's behavior, but instead represent the increasing salience of the long-choice target owing to the passage of time.

Figure 3D provides a closer look at the activity during the test cue period. Here we have normalized the responses to the average activity in the 200 ms epoch that immediately preceded the test cue. This maneuver allows us to superimpose the responses for the short-in-RF and long-in-RF geometries at the beginning of the timing operation. The plot illustrates important features of the timing response. For both target geometries, there is a brief depression of activity (arrow) ~ 125 ms after the fixation spot changes color, marking the beginning of the test cue. This depression is similar in magnitude when expressed as a percentage change in firing rate ($\sim 7\%$ of the baseline level; CI: 4.1%–9.5%, $p < 10^{-5}$, t test). This is followed by a rise in activity that also appears to be similar, in relative terms, for both target geometries, suggesting that this enhancement may represent some common initialization event. Only after ~ 200 –300 ms is there a relative increase or decrease in activity, which parallels the evolving likelihood that the long- or short-choice target will become the appropriate choice. Again, it is important to note the gradual nature of these changes late in the test cue period, despite the fact that all trials will end in the same long choice.

Further dissociation between the monkey's eye movement response and elapsed time is evident on trials when the monkey reports the wrong duration. These errors occurred frequently when the cue duration was similar to the standard. Figure 4 shows the neural activity accompanying cue durations just shorter or just longer than the 800 ms standard. Here we continue to use color to indicate the configuration of the choice targets while indicating errors with dashed lines (correct trials are

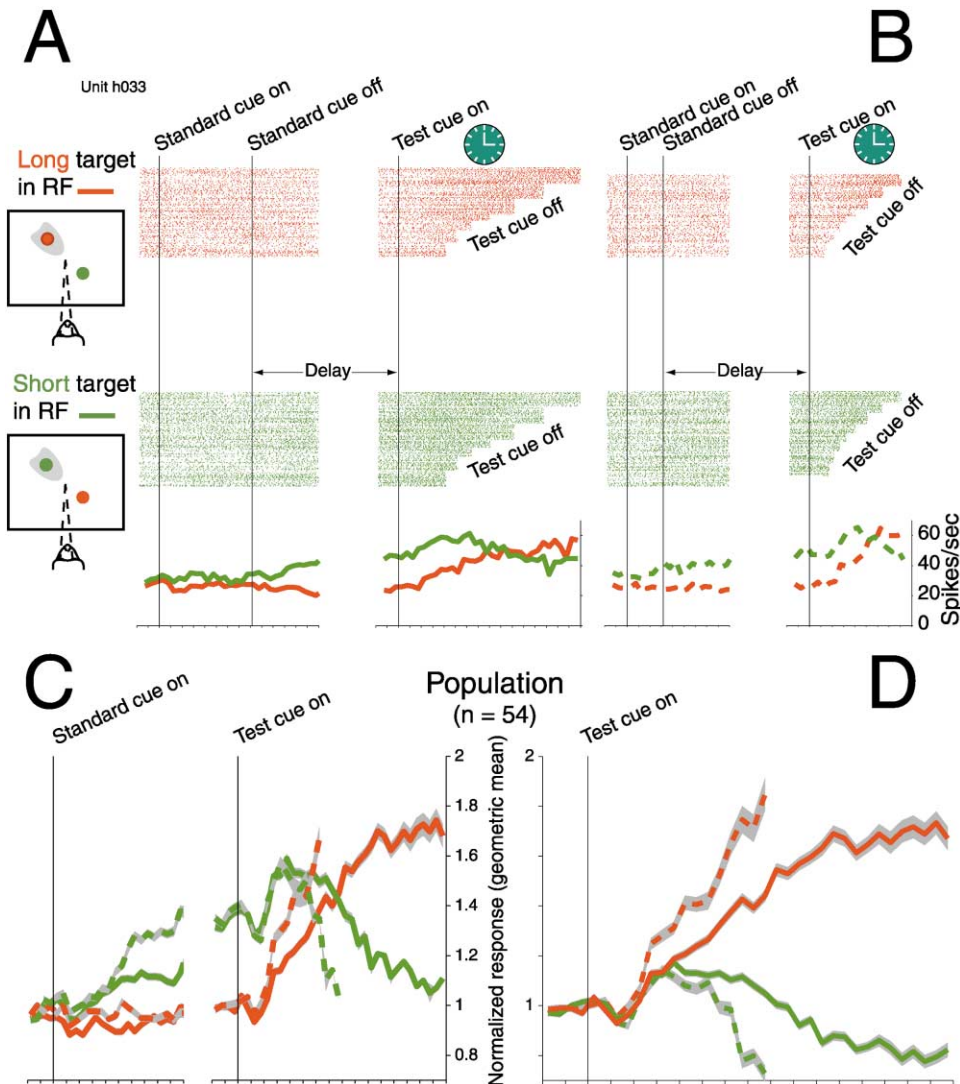


Figure 3. LIP Responses during Time Discrimination

The two target configurations are indicated by the cartoons on the left: either the short-choice target (green) or the long-choice target (red) is in the neuron's RF (gray).

(A) Single neuron responses using the 800 ms standard cue (same neuron as in Figure 2B). Spike rasters are ordered by the duration of the test cue; color indicates whether the short- or long-choice target is in the RF. Responses are aligned to the onset of the standard and test cues. Curves show peri-event averaged spike rates (bin width = 50 ms). Note that fewer trials contribute to the response averages at longer test cue durations. The clock icons indicate the epoch in which the monkey is judging elapsed time. Error trials are not included in this figure. Horizontal tick marks represent 100 ms increments.

(B) Responses from the same neuron during comparison to the 316 ms standard duration.

(C) Average response from 54 LIP neurons. Responses from each cell were normalized to the mean spike rate measured during exposure to the standard cue using both target configurations and both standard durations. Solid and dashed curves represent blocks using the 800 and 316 ms standard, respectively. Shading indicates standard errors of the normalized rate functions. Only correct choices are shown for cue durations not equal to the standard.

(D) Change in activity relative to the spike rate at the beginning of the test cue period. Here, normalization is performed separately for each target configuration and standard duration so that the time course can be compared directly from a common level. See text for details.

“short” in Figure 4A and “long” in Figure 4B). Notice that the configuration of choice targets dominates the pattern of response early in the test cue period—curves representing the same target configuration are near each other—whereas the actual choice dominates the responses after the test cue has been extinguished and through the delay period—curves representing the same eye movement are near each other.

The pattern of responses in Figure 4 allows us to appreciate a representation of elapsed time in a way that is partly dissociable from the monkey's ultimate categorization and action. Consider the trials in which the long choice target is in the neuron's RF, but the monkey chooses short. In Figure 4A these are correct choices, shown by the solid red curve. Although the monkey chose the target outside the RF, the response

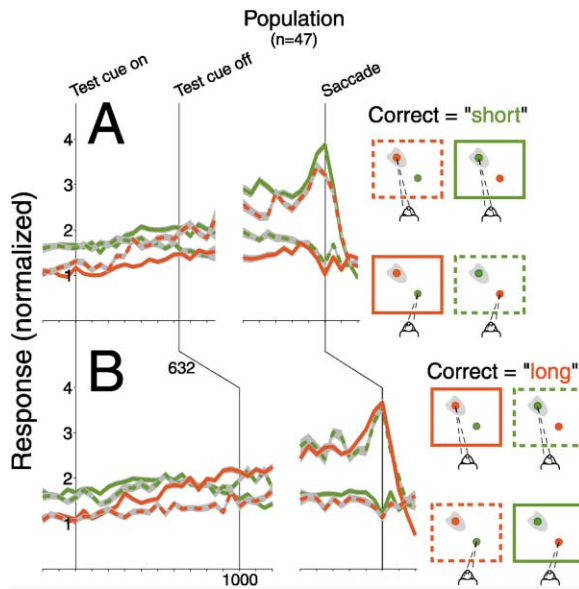


Figure 4. LIP Responses on Correct and Error Trials for All Neurons with a Defined Bisection Point (τ_n) at the 800 ms Standard

Average responses are shown during presentation of the test cue and in the final delay period preceding the monkey's eye movement. (A) Responses on trials in which the monkey compared a 632 ms test cue to the 800 ms standard. Solid curves show responses on trials in which the monkey correctly chose "short," resulting in an eye movement to the RF (green) or away from the RF (red). Dashed curves show responses on trials in which the monkey incorrectly chose "long," resulting in an eye movement to the RF (red) or away from the RF (green).

(B) Responses on trials in which the monkey compared a 1000 ms test cue to the 800 ms standard. Solid curves show responses on trials in which the monkey correctly chose "long," resulting in an eye movement to the RF (red) or away from the RF (green). Dashed curves show responses on trials in which the monkey incorrectly chose "short," resulting in an eye movement to the RF (green) or away from the RF (red). Tick marks on the x axis are separated by 100 ms increments. Shading indicates standard errors of the normalized rate functions.

grew by 49% on average over the course of the 632 ms test cue period (CI: 40%–59%, $p < 10^{-8}$). In Figure 4B, the same combination of target position and short choice gives rise to errors, shown by the dashed red curve. Again, despite the monkey's choosing the target outside the RF, the response grew by 26% over the 1 s test cue period (CI: 11%–40%, $p < 10^{-6}$). The key observation is that the response marks the passage of time, reflecting the increasing salience of the long-choice target even though the monkey does not select this target for its eye movement response.

The time-dependent evolution of activity during the test period contrasts markedly with the pattern of activity during the delay period after the test cue was extinguished. The activity preceding the eye movement response simply indicated the monkey's impending choice (Figure 4, right portion of responses). When the monkeys chose the target in the RF, the neural response was large, regardless of whether the choice was correct or not. This activity resembles the pattern of response seen on the simple delayed eye movement task (Figures 2B and 2C). It is simply an indicator of which target the monkey has chosen.

Naturally, we wondered whether the neural responses could explain the monkey's performance on the timing task. To address this issue, we compared the responses measured when the long-choice target was in the neuron's RF to the responses measured when the short-choice target was in the RF. The separation of these response distributions can be used to estimate how often the neuron assigns greater salience to the long-choice target. This is the probability that a pair of responses drawn from the two distributions would favor the long-choice target, which is conveniently estimated using signal detection theory (Green and Swets, 1966; Parker and Newsome, 1998) (see Experimental Procedures). We refer to this as the probability that the neuron "reports" long.

The resulting neurometric timing functions for the same example neuron are shown in Figure 5A. When the test cue was first turned on, the larger responses were associated with the short-choice target in the RF, leading to a low probability that the neuron reports long. As time elapsed, the responses began to favor the long-choice target. For trials in which the cue was shown for the longest durations, the larger neural responses were associated with the long-choice target in the RF, leading to a higher probability that the neuron reports long. The neurometric function passes through $P = 0.5$ at the neural bisection point, τ_n . For the experiment depicted in Figure 5A, τ_n was 583 and 907 ms when the monkey discriminated time relative to the 316 and 800 ms standards, respectively.

Both neurons and monkeys provided reasonably accurate estimates of the duration of the standard cue. The scatter plot (Figure 5B) shows the distribution of neural bisection points from all 54 neurons, plotted against the bisection points derived from the monkeys' behavior on the same experiments. The neural and behavioral bisection points form two clusters near the standard durations, indicating that estimates of elapsed time furnished by the neuron and the monkey are both affected by the duration of the standard. The neural bisection points were slightly delayed when compared to the behavioral bisection points, especially with the 316 ms standard (47.4 ± 32 ms longer with the 800 ms standard, $p = 0.15$; 88.3 ± 26.5 ms longer with the 316 ms standard, $p < 0.002$). There was considerable variability in both the neural and behavioral bisection points, but from experiment to experiment, there was no obvious relationship between neural and behavioral measurements (see Table 1). The lack of correlation implies that the neurons do not merely indicate the monkeys' eye movement response.

While the neurons in our sample furnished a reasonable estimate of the standard duration, they were far less sensitive to the passage of time than the monkey. For example, the thresholds estimated from the neurometric functions in Figure 5A (θ_n ; see Experimental Procedures) were 163.9 and 356.9 ms with the short and long standard, respectively—much larger than the behavioral thresholds measured in the same experiment (93.3 and 110.8 ms). Indeed, the discrepancy in sensitivity is even greater considering that this neuron only achieved accuracy levels of $\sim 70\%$ for the same test cues that the monkey judged correctly on over 90% of trials. The scatter plot in Figure 5C illustrates this general

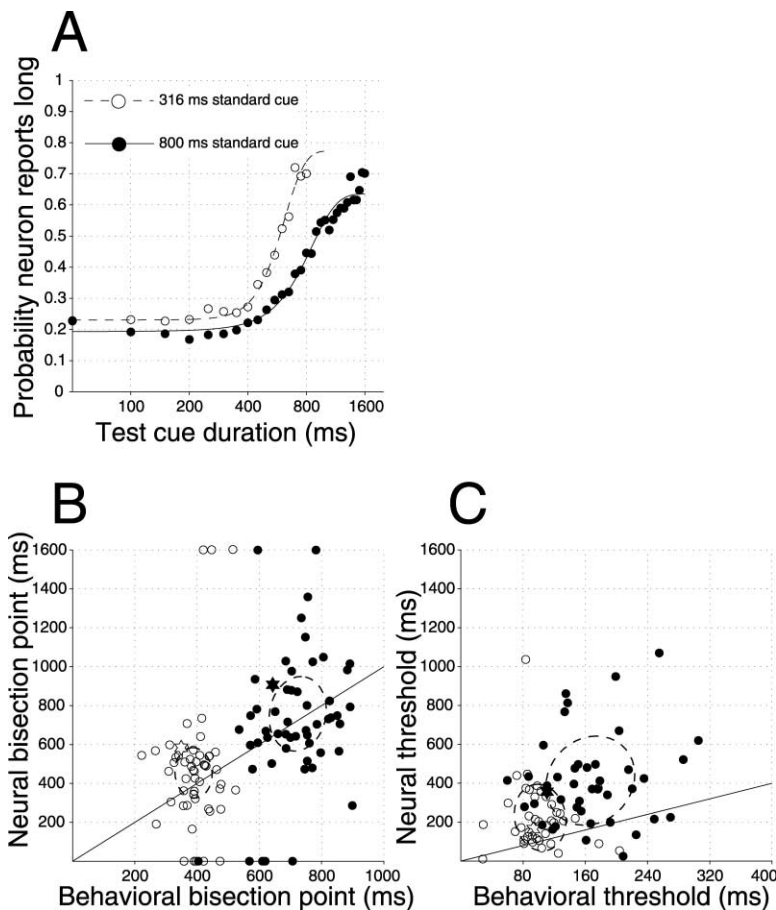


Figure 5. The Capacity of Single Neurons to Discriminate Time

(A) Neurometric function for one neuron (same neuron as in previous figures). The neuron “reports” long if a random sample of its response at the time indicated is greater when the long-choice target is in the RF (open symbols, 316 ms standard; closed symbols, 800 ms standard). Sigmoid curves are best fitting cumulative normal distributions (see text for details).

(B) Comparison of neural and behavioral bisection points. Each experiment ($n = 54$) contributes two points to the scatter plot, one for each standard duration (open symbols, 316 ms standard; closed symbols, 800 ms standard). Stars identify the neuron depicted in (A). The outliers along the bottom of the plot show cases in which the neuron failed to discriminate the choice targets at the beginning of the test cue; outliers along the top of the plot represent failure to discriminate by the end of the longest test cue. Dashed ellipses are the bivariate normal approximations to the remaining data (unit standard deviation contour lines).

(C) Comparison of neural and behavioral thresholds. Same conventions as in (B). Only experiments with a defined τ_n for both standard durations are shown ($n = 42$).

tendency and reveals that the neural thresholds are more variable than those obtained behaviorally. Nonetheless, there is one important similarity between neural and behavioral thresholds that is worth noting. While the average ratios θ_n/τ_n are larger than the corresponding behavioral ratios, they too remained relatively constant across standard durations (Table 1; $p = 0.30$, paired t test after log transform). Thus, neural thresholds also show some consistency with Weber’s law.

Time Discrimination by Neural Ensembles

It is reasonable to expect that time discrimination by a monkey would be superior to what a single LIP neuron could achieve. If the monkey bases its judgment of elapsed time on the activity of an ensemble of neurons, then the sensitivity of the ensemble rather than the single neuron would be expected to compare more favorably to what was observed behaviorally. One simple idea is that the monkey judges time by comparing the average activity from pools of neurons that represent the visual salience of the short- and long-choice targets: the larger value determines the monkey’s choice. It is relatively straightforward to estimate the performance of such a model (Shadlen et al., 1996).

We used our data to construct pools of neurons that signified the short- or the long-choice target as salient. Our recordings furnished the expected response from each neuron as a function of time, along with the associated variability. We lacked only two pieces of informa-

tion: the size of the pools (N_{short} and N_{long}) and the degree to which variability is shared among the neurons (covariance). We assumed a weak correlation between neurons with the same receptive field ($r = 0.15$), a value that is common for pairs of neurons with similar response properties in visual, somatosensory, and motor cortex (Bair et al., 2001; Gawne and Richmond, 1993; van Kan et al., 1985; Lee et al., 1998; Salinas et al., 2000; Zohary et al., 1994). As previously shown, so long as the covariance is not negligible (on average), pool size is immaterial for $N > \sim 50$ –100 (Shadlen et al., 1996; Shadlen and Newsome, 1998; Zohary et al., 1994). We therefore calculated the ensemble averages using pools of 100 neurons by sampling our data set randomly with replacement (see Experimental Procedures). These averages along with their associated variability were used to calculate the probability that the ensemble “reports” long as a function of test cue duration. The resulting “ensemble neurometric functions” (Figure 6) show the performance that would ensue if an ideal observer consulted the ensemble of LIP neurons to tell time.

Unlike the neurometric functions from single neurons, the ensemble neurometric functions (Figure 6) are roughly parallel to the psychometric functions and thus reflect a degree of sensitivity to the passage of time that is comparable to the sensitivity of the monkeys. The ensemble neural thresholds from these functions are 126 and 181 ms for the short and long standard, respectively, which is within the range of thresholds observed

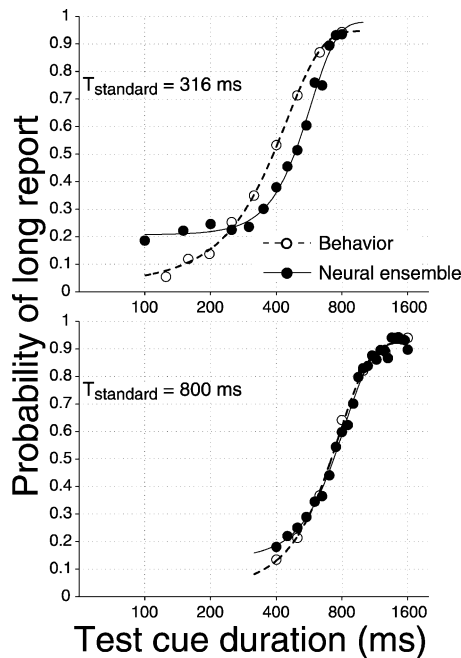


Figure 6. Predicted Performance Based on an Ensemble of 100 or More LIP Neurons

Behavioral functions (psychometric) are based on trials from all 54 experiments. The ensemble “reports” long if a random sample of the average response from 100 neurons is greater when the long-choice target is in the RF. Ensemble responses were generated using the measured spike rates and associated variance in our data set. Each ensemble response was simulated by drawing 100 samples from the data using a method that introduces weak covariance among the samples (average pairwise correlation coefficient = 0.15). The weak covariance ensures that ensemble size >100 would not affect the neurometric function.

for behavior (see Figure 5C and Table 1). These estimates were obtained by comparing spike rates calculated in epochs of 150 ms long. Higher thresholds would be obtained using shorter epochs (e.g., ensemble thresholds using 50 ms worth of spike discharge are 137 and 249 ms for the short and long standards, respectively), but the correspondence between neural and behavioral sensitivity remains reasonable. Interestingly, the ensemble neurometric functions lag the psychometric functions by 25 and 100 ms for the short and long standards, respectively (see also Figure 5B). A lag of this magnitude is expected because of latencies in the processing of visual information related to the offset of the test cue. For example, consider the test cue that the monkey judges as long or short with equal probability (i.e., τ_b). Offset of this test cue would be represented in the brain after a short latency, that is, near the time of the neural bisection point (τ_n). With this caveat in mind, it appears that the ensemble LIP activity can account for both the sensitivity and accuracy of the monkeys’ judgments of elapsed time.

Discussion

We have shown that the representation of elapsed time that can be inferred from ensembles of neurons in area

LIP approximates the fidelity of the monkey’s timing behavior. This suggests that the monkey could base its judgment of time on the discharge of neurons with properties like the ones we observed. The demonstration that LIP represents the passage of time does not imply that the parietal cortex is responsible for the perception of time. Rather, it is likely that time is represented in many structures in the brain. Our observations are consistent with recent neuroimaging and clinical studies that implicate the parietal lobe in timing behavior (Harrington et al., 1998; Onoe et al., 2001; Rao et al., 2001; Schubotz et al., 2000). What is remarkable is that the representation of time is present in single neurons in the brain.

The parietal lobe—and LIP in particular—is thought to play a role in the allocation of spatial attention (Colby and Goldberg, 1999), the planning of eye movements (Andersen, 1997; Mazzoni et al., 1996; Snyder et al., 2000), and the formation of decisions (Shadlen and Newsome, 2001). To control such processes, it is sensible for the brain to register the time that information is likely to be relevant and by when a plan for action should be established (Ghose and Maunsell, 2002). In our task, elapsed time has a direct bearing on the relative importance of the visual field containing the short- or long-choice target. As time passes, the importance of the short-choice target gives way to the long-choice target. In accordance with this schedule, neurons in LIP can be said to allocate attention, plan a future eye movement, or represent the monkey’s decision to choose one or the other target. The representation of elapsed time in LIP may be limited to this pragmatic framework in much the same way that the representation of space in LIP has been interpreted in terms of motor planning (Andersen, 1997; Rizzolatti et al., 1997; Snyder et al., 2000). Based on our experiments, we are unable to tell whether the representation of time in LIP can be used to control other processes besides allocation of attention and gaze planning. It is possible that many association areas keep track of elapsed time relative to behaviorally relevant epochs, each representing its own inherent “rhythm.”

If the representation of time in LIP can be interpreted as a gradual shifting of spatial attention or motor planning, why conclude that time is represented at all? In what follows, we evaluate alternative explanations for the data, which do not require an explicit representation of time.

Alternative Explanations

Motor Planning

As exemplified in Figure 2D, many neurons in LIP respond during a delay period between an instruction to move the eyes and a go signal. Can the responses observed in the timing task be explained as a byproduct of oculomotor planning, without invoking a representation of elapsed time? According to this idea, the responses merely represent the monkey’s plan to make an eye movement to the short- or long-choice target. This explanation fails to explain two observations.

First, the idea predicts a correlation between neural and behavioral timing functions obtained from the same experiments, which we did not detect (Figures 5B and 5C; Table 1). If the neuron is merely indicating where

the monkey will look next, then the neuron should predict the monkey's psychometric function. For example, neurometric functions derived from activity in the final 100 ms epoch of the delay period were correlated with the monkey's behavior ($r = 0.55$ and 0.48 for 800 ms standard and 316 ms standard, respectively; $p < 0.006$). Even if neurons were to indicate the monkey's eye movements imperfectly during the test cue period, the bisection points derived from neuron and behavior should exhibit some tendency to covary, but there is no such tendency in the data (Figure 5B).

Second, the motor planning idea fails to explain the pattern of activity evident in the beginning of the test cue period: The activity favors the short-choice target, whereas there is an equal chance that the trial will result in an eye movement to either target. While it is true that the passage of time would be expected to promote a plan to choose the long target, so long as the test cue remains on, the answer to the question, "Which is the likely eye movement target?" should never favor the short-choice target (Figure 7A). It seems instead that that the activity answers the question "What time is it now?" (Figure 7B). LIP favors the short-choice target at the beginning of the test cue period because it is the more salient target.

Attention

Neurons in LIP are also thought to represent the locus of spatial attention (Bisley and Goldberg, 2003). Accordingly, the delay period activity exemplified in Figure 2D could represent a shift in spatial attention to the neuron's response field. The distinction between attention to a location and intention to move the eyes can be thorny (Snyder et al., 1998). For our purposes, we must consider the possibility that the pattern of responses observed in the timing task is simply a reflection of a shift in attention from the short-choice target early in the trial to the long-choice target later. This idea can explain the pattern of activity at the beginning of the test cue period, for while the monkey has no incentive to make an eye movement to the short-choice target, it is nonetheless the more salient target early in the test cue period. However, so long as attending to a target implies some tendency to choose this target, the attention idea suffers from the same limitation as *motor planning*. If the neural activity indicates that the monkey's attention is directed to the short- or the long-choice target, then it should predict the monkey's behavioral response. The representation of attention might be imperfect but at the very least we would expect to see a correlation between behavioral and neural measurements of performance (e.g., bisection points) across experimental sessions, but we did not (Figure 5B).

There is a version of the attention explanation that seems entirely compatible with our data. It is that the monkey attends first to the short-choice target and then gradually shifts attention to the long-choice target. At the neural bisection point, attention is allocated equally to both targets. This interpretation implies that time is represented in LIP and suggests that at a minimum it is used to allocate spatial attention.

Decision Outcome

Neurons in LIP are also thought to represent the formation and outcome of decisions that result in an eye movement response (Platt and Glimcher, 1999; Shadlen and

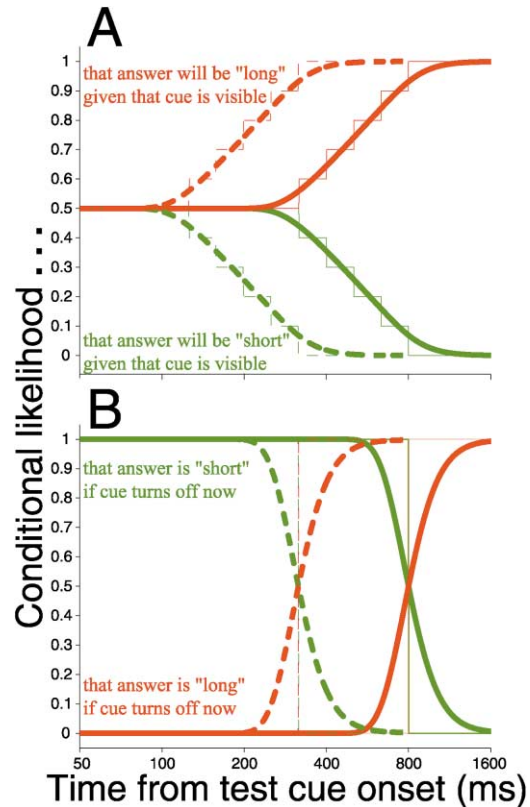


Figure 7. Theoretical Subjective and Objective Timing Functions (A) The probability that the cue will be shorter (green) or longer (red) than the standard, given that it is still visible. Thin lines show the objective likelihoods (step functions), based on the possible cue durations. Thick curves are subjective estimates of likelihood based on the assumption that the elapsed time is known with uncertainty (subjective time described a normal probability distribution with $\mu = t$ and $\sigma = 0.2t$, i.e., Weber fraction 20%). Solid, 800 ms standard; dashed, 316 ms standard. These curves represent the answer to the question, "Which target will be chosen?" Note the discrepancy between these theoretical curves and the neuronal responses. (B) The probability that the cue duration is shorter (green) or longer (red) than the standard if it were to terminate in the next moment. Thin lines (step functions) show the objective categorization in favor of long or short. Solid curves are subjective estimates of these categories based on the assumption that the elapsed time is known with uncertainty (subjective time as in [A]). These curves represent the answer to the question, "What time is it now?" The criss-crossed pattern is characteristic of the neural responses in area LIP. Solid, 800 ms standard; dashed, 316 ms standard.

Newsome, 1996, 2001; Toth and Assad, 2002; Roitman and Shadlen, 2002; Gold and Shadlen, 2001). Perhaps the brain computes elapsed time in other brain circuitry and merely transmits the decision, "short" or "long," to LIP. According to this idea, when the long-choice target is in the neuron's RF, the response would remain in a low state until sufficient time has elapsed to cause a shift in judgment to "long," at which point the response would change to a high state. If such a change were to occur at different times on different trials, the average spike rate across many trials could appear gradual (as in Figure 3C; red curves), because the mixture of low state and high state trials would favor the latter with increasing cue duration.

Several observations render this explanation unlikely. First, if the intermediate values observed in our response averages comprise a mixture of low and high values, then the activity near the neural bisection point would comprise a mixture of relatively low responses like those at the beginning of the test period and relatively high responses like those at the beginning of the delay period. In fact, we failed to detect such a bimodal distribution ($p > 0.3$, Harnad's dip test; see Experimental Procedures). Our failure to detect this is probably not for lack of sensitivity, since the same analysis detects a bimodal distribution of responses in a control distribution constructed from the rates in the delay period associated with the two target choices ($p < 0.03$). Moreover, the distribution of spike counts at the bisection point exhibits considerably lower variance than would be expected from a mixture of low and high levels of activity seen at the beginning and end of the test cue (24% less; CI: 17%–32%, $p < 0.001$; χ^2 test). These observations indicate that the intermediate level of activity accompanying the passage of time is unlikely to reflect a mixture of "short" and "long" states. Instead, the intermediate levels of activity would seem to represent the uncertainty about elapsed time with respect to the standard.

Second, if LIP reflects decision outcome, then activity before the change from low to high rate should not vary systematically with the passage of time. To test this, we examined individual trials for evidence of a change from a low to a high rate, focusing on the trials that ended in long choices (Figure 3D, solid red curve). On each trial, we used a maximum likelihood procedure to identify the moment (t_Δ) that the spike rate changed from low to high (Commenges et al., 1986). Even for the subset of trials in which the change occurred later in the test period (571 of 2149 trials, $t_\Delta > 800$ ms), the spike rate increased monotonically early on (e.g., the rate changed by 11.4 sp/s² during the 400 ms epoch beginning 100 ms after cue onset; CI: 6.8–16.1 sp/s²; $p < 0.0002$). Contrary to the "decision-outcome" hypothesis, the spike rate was not constant as a function of time before the change point.

A third reason for rejecting the idea that LIP merely reflects the outcome of the monkey's decision about time comes from examination of error trials (Figure 4). During the test-cue period, the activity was similar on trials that the monkey would later classify differently. If the activity reflects the monkey's decision, then sorting the trials by choice should have exposed striking differences in the response, as it does in the delay period. Together, these observations indicate that the evolution of LIP activity during timing is unlikely to represent the outcome of a binary decision about time. The pattern of activity is more consistent with a gradual shift in the monkey's allocation of attention or the relative salience of the choice targets. Importantly, these graded changes in activity mimic the monkey's uncertainty about elapsed time.

Deciphering the neural basis of time perception has been a major challenge for neuroscience (Gibbon et al., 1997; Ivry, 1996; Meck, 1996). Our findings reveal that elapsed time is represented by neurons in posterior parietal area LIP. Presumably, this is because the passage of time renders a visual target more or less salient for purposes of allocating attention and planning eye move-

ments. It seems unlikely that LIP plays a unique role in time perception. For example, we would expect neurons in nearby parietal areas AIP (Sakata et al., 1995) and the parietal reach region (Snyder et al., 2000) to represent time when it is pertinent to pincer grasp and reaching. In general, time is likely to be represented in all association areas that must evaluate when sensory information is behaviorally relevant or when an action must ensue. More direct tests using lesions and electrical stimulation will be required to determine whether the parietal cortex is essential for time-keeping in this context.

Experimental Procedures

Electrophysiology

Two adult rhesus monkeys (monkey H, female, 5.3 kg; monkey B, female, 4.6 kg) were implanted with an eye coil, head-holding device, and recording cylinder suitable for magnetic resonance imaging (Crist Instrument, Damascus, MD). Microelectrodes were advanced through a stainless steel guide tube into the brain and directed toward the lateral bank of the intraparietal sulcus (area LIP). Electrode penetrations were registered with magnetic resonance images (Figure 2A) to confirm that recordings were made in area LIP (Van Essen et al., 2001). All procedures and treatments were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and approved by the University of Washington Animal Care Committee.

We used standard methods for single unit extracellular recording, as previously described (Kim and Shadlen, 1999). Single units were isolated using a dual voltage-time window discriminator (Bak Electronics, Germantown, MD). The times of action potentials were marked as events with 1 ms precision and stored to disk for off-line analysis. Horizontal and vertical eye position was measured with a scleral search coil (C-N-C Engineering) and stored to disk (250 Hz) for off-line analysis. We screened neurons using a memory-saccade task (Hikosaka and Wurtz, 1983). We studied all neurons with spatially selective activity in the memory delay period (Bracewell et al., 1996; Shadlen and Newsome, 2001). All physiological data reported in this paper were acquired from neurons that remained spatially selective during the timing task, responding significantly more during the presaccadic delay period that preceded eye movements to the neuron's RF ($p < 0.05$; t test).

Time Discrimination Task

A trial began with the simultaneous onset of a blue fixation point (FP) and two choice targets displayed on the computer monitor (see Figure 1; Power Macintosh 7500 running MATLAB and using the extensions provided by the high-level Psychophysics Toolbox [Brainard, 1997]). On any trial, one target appeared in the neuron's RF and the other target appeared 180° away, opposite the FP. The locations of the short- and long-choice targets were alternated randomly across trials so that for test cues of any duration, an approximately equal number of trials was collected with the short- and long-choice target in the neuron's RF. The monkey fixated a blue spot (FP) at the center of the video monitor. Shortly after fixation (400–1000 ms), the FP turned white for either 316 or 800 ms ("standard cue"). Following a delay period (500–1000 ms), the FP turned white again, this time for a variable duration to mark the "test cue." After a second delay period (500–1000 ms for monkey H; 100–500 ms for monkey B), the blue FP was extinguished, which instructed the monkey to indicate its judgment of time. The monkey was required to make an eye movement to the green (short-choice) target if the test cue was judged to be shorter in duration than the standard, and to the red (long-choice) target if the test cue was judged to be longer than the standard. The monkey received a liquid reward for a correct choice and was rewarded randomly on trials in which the test and standard cues were of equal duration.

Experiments using the two standard durations were performed in alternating blocks of trials. On each trial the duration of the test cue was randomly chosen from a set of 7–9 durations that varied in 0.1 log unit increments about the standard. Trials in which the monkey

broke fixation or failed to make an eye movement within 500 ms after FP offset were excluded from the analyses. The blocked design does not allow us to draw inferences about how the monkeys use the information presented during viewing of the standard cue, which was the same on each trial in the block. In particular, we do not presume that the monkeys held a representation of the standard cue during the period before the test cue (Hernández et al., 1997). Our analyses are therefore restricted to the representation of elapsed time during the test cue period.

Data Analysis

To characterize the monkey's ability to estimate time, we plotted the probability of making an eye movement to the long-choice target for a given test cue duration and fit the data with a cumulative normal distribution (Probit analysis; Finney, 1952). The mean, standard deviation, and upper and lower asymptotes of the fitted curve were free parameters. The bisection point, τ , is the time at which short and long choices are equally likely: $P(\tau) = 0.5$. The threshold, θ , was estimated from the slope of the sigmoid at τ :

$$\theta = \frac{\sqrt{2\pi}}{4k} \sigma,$$

where σ is the standard deviation of the fitted cumulative normal, and k is the difference between the curve's upper and lower asymptotes ($k_{\max} = 1$). For a sigmoid bound by 0 and 1, θ is approximately half the interquartile range (i.e., $P(\tau + \theta) \approx 0.75$). When asymptotic performance is not perfect ($k < 1$), as in the sigmoid fits to neural data, θ^{-1} still estimates the sensitivity to change in time near the bisection point whereas σ^{-1} does not.

We computed the probability that a neuron "reports" long by comparing its activity when the short- or the long-choice target was in its RF. This is the probability that a random draw from the long-choice-target-in-RF distribution is larger than a random draw from the short-target-in-RF distribution, which is given by the area under an ROC defined by the two distributions (Britten et al., 1992; Green and Swets, 1966). We performed this analysis as a function of time during the test cue, using spike rates calculated in 150 ms epochs. Only correct trials and ambiguous trials (in which the test cue duration was equal to the standard) were included in this analysis. The resulting neurometric functions were fit by cumulative normal functions, as above. Inclusion of error trials did not affect the estimation of bisection points, but led to a small rise in threshold (decreased neural sensitivity). For some comparative analyses, we also computed neurometric functions from delay period activity. For these analyses, we used data from all trials.

We considered the possibility that the gradual increase in spike rate seen in Figures 3A–3C (red curves) might be explained by a change from a low to a high rate of firing—the change occurring at a different time on any one trial. We searched each trial for such a change using the method of maximum likelihood introduced by Commenges and Seal (Commenges et al., 1986). For each trial, we obtained the log-likelihood ratio (Λ) that would favor the existence of a change point over a fixed spike rate. We used Monte Carlo methods to estimate the distribution of Λ under the null hypothesis that spikes occurred at random intervals in accordance with the average rate function (as in Figure 3). The surrogate spike trains were generated using the method described in Oram et al. (1999). A change point was deemed significant if the surrogate spike trains produced higher values of Λ with probability less than 0.05. We also examined the distribution of spike rates at the bisection point for evidence of bimodality using a modified version of Hartigan's dip test (Hartigan and Hartigan, 1985). To apply the test to discrete spike count data, we added a random offset, ϵ , to each normalized count, where ϵ is a uniformly distributed random number between 0 and the median difference between the (unperturbed) sorted values. The p values reported in the text are averages of 10 calculations, which employ different random values, ϵ . This technique produces sensible results on other unimodal, discrete distributions (e.g., Poisson).

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